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1 **Facultative predation and scavenging by mammalian**  
2 **carnivores: seasonal, regional and intra-guild**  
3 **comparisons**

4

5 **ABSTRACT**

6 **1.** The extent to which vertebrate carnivores shift facultatively between predation and  
7 scavenging has recently been emphasized. In this article we propose as a null  
8 foundation that all carnivores have to do is wait until animals eventually succumb to  
9 the debilitating effects of advancing age. However, this may be insufficient,  
10 recognizing the intense competition among other scavengers and decomposers for  
11 the rich food. Moreover, the availability of carcasses of animals dying from causes  
12 besides predation varies seasonally, so carnivores must be adapted to exploit other  
13 sources of food in order to survive through the seasonal cycle.

14 **2.** We explore how mammalian carnivores cope with seasonality in carrion supply  
15 and prey vulnerability to predation. We focus mainly on large carnivores and  
16 ungulates, and we compare ecological communities living in northern temperate and  
17 African savanna ecosystems.

18 **3.** When carrion is scarce, carnivores can (i) take advantage of temporarily  
19 vulnerable segments of prey populations, such as newborn young, heavily pregnant  
20 females and males distracted or debilitated by reproductive activities, (ii) switch to  
21 carcass remains left by or stolen from other carnivores, or (iii) exploit small animals  
22 and non-animal food sources.

23 **4.** Relationships between carnivores tending towards predation or scavenging can be  
24 both competitive and facilitatory. For instance, top-carnivores can provide a quite  
25 constant supply of carcasses throughout the year, which crucially subsidizes  
26 scavengers in the seasons when carrion availability by other causes is low.

27 Alterations of seasonal patterns due to human-caused environmental change may  
28 enhance the role of top-carnivores as buffers of anthropogenic perturbations of  
29 natural processes.

30 **5.** Megaherbivores, which are not normally regarded as prey but can indeed provide  
31 huge carrion subsidies, may strongly influence the future interspecific interactions  
32 between carnivores and the proportion of food flowing towards scavenging relative to  
33 predation.

34

35 *Keywords:* African savannas, carrion supply, competition, facilitation, global warming,  
36 megaherbivore, northern temperate ecosystems, prey vulnerability, seasonality

37

38 Running head: Predation versus scavenging in carnivores

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45

46

46 **INTRODUCTION**

47 All animals die eventually, and their carcasses provide a food source for scavengers.  
48 By definition, scavengers feed on the remains (i.e. carrion) of animals that have died,  
49 while predators kill animals in order to feed on the resulting carcasses. Nevertheless,  
50 vertebrates traditionally labelled predators usually do not pass by opportunities to  
51 consume carcasses when encountered (DeVault et al. 2003, Selva et al. 2005,  
52 Wilson & Wolkovich 2011); indeed, what we find in nature is a quite continuous  
53 gradient from the most genuine predators that rarely eat dead animals (e.g. cheetah  
54 *Acinonyx jubatus*) to those mostly consuming carrion (e.g. brown hyaena *Hyaena*  
55 *brunnea*; e.g. Skinner & Chimimba 2005). Therefore, the conventional distinction  
56 between predators and scavengers may be misleading with regard to both the inter-  
57 specific interactions and the energy fluxes taking place within food webs.

58 Schaller (1972) distinguished four ways whereby carnivores secure their food:  
59 (1) Additive predation (i.e. killing healthy animals); (2) Compensatory predation (i.e.  
60 preying on young, old or sick animals vulnerable to mortality from other causes,  
61 thereby promoting the survival of the remainder of the prey population); (3)  
62 Kleptoparasitism (i.e. displacing other carnivores from their kills); (4) Scavenging (i.e.  
63 feeding solely on animals that have died from disease, malnutrition or other causes,  
64 or on the remains of predator kills). Individual carnivores can exhibit several or even  
65 all of these feeding patterns, which shows that there may be a continuum between  
66 predatory versus scavenging strategies not only at the inter- but also at the intra-  
67 specific level.

68 In this article we propose as a null foundation that all carnivores have to do to  
69 feed is wait until animals eventually succumb to the debilitating effects of advancing  
70 age. In practice this is untenable, recognizing the intense competition among other  
71 scavengers and decomposers for the rich food constituted by animal body tissues  
72 (Wilson & Wolkovich 2011). Hence, helping animals die a little sooner can gain prior  
73 access to the meat. However, the energy costs associated with hunting are high,

74 especially for large mammals; for instance, transport costs for the largest carnivores  
75 (lions –*Panthera leo*– and polar bears –*Ursus maritimus*–) are 2-3 times higher than  
76 expected for their size (Carbone et al. 2007). The challenge that carnivores face is  
77 how to secure a regular supply of food when the susceptibility of animals to die or be  
78 killed varies seasonally and spatially. As a result, most large mammalian carnivores  
79 shift facultatively between hunting and scavenging depending on seasonal and  
80 regional variation in the susceptibility of their prey to mortality.

81         Seasonal variation in the availability of food is a central theme in the ecology  
82 of herbivores (Owen-Smith 2002). However, its role in carnivory has not been  
83 adequately addressed by previous reviews (Cortés-Avizanda et al. 2009, DeVault et  
84 al. 2011, Wilson & Wolkovich 2011), and there are important consequences for intra-  
85 guild relationships among carnivores as well as for biomass pathways through food  
86 webs. Seasonal variation in high northern latitudes is governed by temperature  
87 variation and snow accumulation, whereas in more tropical latitudes rainfall and  
88 hence surface water availability is the dominant influence. Seasonal variation in the  
89 vulnerability of their prey to being killed has implications for the conservation of  
90 carnivores in human-modified ecosystems. Those perceived as predators are largely  
91 eliminated in order to protect domestic animals (e.g. Gittleman et al. 2001), and  
92 human hunting can substantially modify carrion subsidies (e.g. Wilmers et al. 2003).

93         Recent reviews addressing overlaps between scavenging and hunting have  
94 been orientated towards northern ecosystems, which retain somewhat impoverished  
95 remnants of their former carnivore complement (Jędrzejewski et al. 1993, DeVault et  
96 al. 2003, Cortés-Avizanda et al. 2009). Those addressing African ecosystems with  
97 largely intact carnivore assemblages have emphasised predation and its  
98 consequences, rather than the scavenging that also takes place (Sinclair et al. 2003,  
99 Hayward 2006). We aim to balance this oversight by considering how large  
100 mammalian carnivores cope with seasonal variation in food availability through  
101 flexibility in their feeding strategies from strict predation to mainly scavenging. In

102 particular, we address the following questions: (1) How do carnivores cope with the  
103 seasonal period when prey are least vulnerable to mortality?; (2) How does  
104 facultative scavenging or predation affect competitive or facilitative relationships  
105 among carnivores?; (3) How do these patterns differ between depauperate northern  
106 communities and intact African ones?; (4) How do human activities alter trophic  
107 interactions and fluxes through predation versus scavenging?

108

109 **SEASONAL VARIATION IN PREY MORTALITY AND VULNERABILITY TO**  
110 **PREDATION: CARNIVORE RESPONSES**

111 Seasonal variation in food availability for carnivores may be generated in various  
112 ways. In the absence of predators, almost all deaths among adult ungulates in high  
113 northern latitudes occur during the winter months, when food shortages may lead  
114 directly to death or compromise the ability of these animals to withstand thermal  
115 stress (Clutton-Brock & Albon 1982, Coulson et al. 2001). The ability of ungulates to  
116 escape predation is also hampered by deep winter snow, benefitting especially  
117 cursorial predators like grey wolves (Post et al. 1999, Jędrzejewski et al. 2002,  
118 Hebblewhite 2005) and coyotes (*C. latrans*; Bekoff & Wells 1981, Huegel & Rongstad  
119 1985). In the Białowieża Forest in Poland, 25-75% of discovered carcasses of the  
120 various ungulate species had apparently died from causes other than predation,  
121 despite the rich assemblage of predators there (Jędrzejewski et al. 1993). Although  
122 the frozen meat may present an obstacle for some carnivores (Haynes 1982, Selva  
123 et al. 2003), wolverines (*Gulo gulo*) take advantage of the refrigeration provided by  
124 high northern winters by amassing caches of carrion to augment opportunistically  
125 found carcasses (Inman et al. 2012a). Frozen carcasses may become accessible to  
126 other carnivores in a narrow pulse during the spring thaw. Northern ungulates are  
127 generally in worst condition during the transition from winter into spring, when adult  
128 elk can make up the majority of the diet of grey wolves (Metz *et al.* 2012).

129           In African savannas, deaths of herbivores attributed to causes other than  
130 predation are concentrated towards the end of the dry season when food is limiting  
131 (Mduma et al. 1999, Owen-Smith 2008). In Tanzania's Serengeti National Park, 64%  
132 of deaths of wildebeest (*Connochaetes taurinus*) occurred during the course of the  
133 dry season extending through July-December when the shortage of green grass  
134 became accentuated (Mduma et al. 1999). Body size influences the relative  
135 susceptibility of ungulates to starvation rather than predation, but with regional  
136 variation evident. In Serengeti, 75-90% of deaths of ungulates in the size range 170-  
137 250 kg was ascribed to predation, while only 20% of the mortality among buffalo  
138 (*Syncerus caffer*) and giraffe (*Giraffa camelopardis*) was due to predation (Sinclair et  
139 al. 2003). In contrast, in South Africa's Kruger National Park, 94% of found carcasses  
140 of all species weighing less than 1000 kg were attributed to predator kills, and  
141 uneaten carcasses were recorded only during disease outbreaks or severe droughts  
142 (Owen-Smith & Mills 2008). A proportion of the carcasses generated during disease  
143 outbreaks and droughts or extreme winter weather may remain uneaten, apparently  
144 because they become desiccated and lose the water content that most carnivores  
145 depend on from their food, especially under tropical African conditions (Gasaway et  
146 al. 1991, Cooper et al. 1999).

147           Migratory movements also affect the patterns of both ungulate mortality and  
148 vulnerability to predation. In Serengeti, deaths not mediated by predation are  
149 amplified by the huge local concentrations of migrants, saturating the capacity of  
150 resident predators to exploit them. Spotted hyenas (*Crocuta crocuta*) commute long  
151 distances to reach places where these ungulates are concentrated (Hofer & East  
152 1993). Hence, migratory wildebeest, zebra (*Equus quagga*) and Thompson's gazelle  
153 (*Eudorcas thomsonii*) form the majority of spotted hyena's diet in the Serengeti plains  
154 despite only being available there for 26% of the year (Hofer & East 1993). When  
155 these migratory ungulates reach the Kenia's Masai Mara region during the dry  
156 season, they greatly increase the supply of carrion there. The desiccated carcasses

157 help support carnivores after the migrants have left (Cooper et al. 1999). In Africa,  
158 buffalo become most vulnerable to predation on adults when at their weakest during  
159 the transition period around the start of the rains (Owen-Smith 2008).

160 Prey vulnerability, dependent on age and body condition, is especially  
161 important for cursorial predators like wolves (*Canis lupus*), spotted hyenas, wild dogs  
162 (*Lycaon pictus*) and cheetahs, which capture their prey through pursuits limited in the  
163 duration that they can be sustained (FitzGibbon & Fanshawe 1989, Huggard 1994,  
164 Pole et al. 2004). On the other hand, ambush hunters like most felids, which rely on  
165 stalking to within attack distance, are less affected by seasonal variation in the  
166 vulnerability of their prey. For example, cougars (*Puma concolor*) kill mule deer  
167 (*Odocoileus hemionus*) adults in better condition than those captured by grey wolves,  
168 although both species are selective towards calves and old individuals when hunting  
169 larger prey like elk (*Cervus canadensis*; Husseman et al. 2003). African lions also  
170 more successfully catch weakened prey (Sinclair & Arcese 1995).

171 In spring or the early wet season, vulnerable newborn animals are generally  
172 produced, and become a food source for more omnivorous carnivores. Brown (*U.*  
173 *arctos*) and black bears (*U. americanus*) switch to hunting newly born caribou  
174 (*Rangifer tarandus*), elk and moose calves, albeit for only a few weeks (Gasaway et  
175 al. 1992, Mahoney & Schaefer 2002, Swenson et al. 2007, Barber-Meyer et al.  
176 2008). Red foxes (*Vulpes vulpes*) cause much mortality among newborn ungulates  
177 from roe deer (*Capreolus capreolus*; Jarnemo et al. 2004) to reindeer, and  
178 wolverines also become predators on elk in this vulnerable life history stage (Tveraa  
179 et al. 2003, Gustine et al. 2006). Grey wolves concentrate their hunting on elk calves  
180 during summer and autumn and kill newborn bison (*Bos bison*) in early spring (Metz  
181 et al. 2012). Likewise, African carnivores such as lions and even jackals (*C.*  
182 *mesomelas*) take advantage of opportunities to run down juvenile ungulates that are  
183 more easily caught than the adult ungulates that they normally seek (Mills & Shenk  
184 1992, Owen-Smith & Mason 2005, Owen-Smith 2008).



185 Male and female ungulates also show seasonal variation in their relative  
186 susceptibility to predation (Owen-Smith 2008). Females that are heavily pregnant are  
187 less capable of evading predation, and especially vulnerable during parturition  
188 (Molinari-Jobin et al. 2004). Male ungulates compete for mating rights while in prime  
189 condition in autumn after the end of the growing season, thereby exposing  
190 themselves to heightened risks of predation both through injuries sustained in fights  
191 and by isolating themselves from the security of the herd (FitzGibbon 1990a).  
192 Furthermore, the energy invested in rutting behavior leaves these males in a  
193 weakened state after the end of the mating period and hence more vulnerable to  
194 predators (FitzGibbon 1990b). Over the annual cycle, male ungulates invariably incur  
195 higher mortality rates than adult females (Pole et al. 2004, Owen-Smith et al. 2005,  
196 Owen-Smith 2008, Grange et al. 2012).

197 In summary, for predators the lean time of the year is towards the end of the  
198 summer or the rains, after calves have become robust and food remains plentiful  
199 (Fig. 1). Then carnivores have to turn their attention to alternative prey that, despite  
200 their lower meat yield, are more readily available. During summer, coyotes and foxes  
201 commonly hunt hares or mice (Bekoff & Wells 1981, Nellis & Keith 1976, Hamlin et  
202 al. 1984, Patterson et al. 1998), while wolves shift from moose towards beavers  
203 (*Caster canadensis*) on Isle Royale (Peterson & Page 1988), and towards white-  
204 tailed (*O. virginianus*) or mule deer in place of elk in Yellowstone National Park and  
205 elsewhere (Metz et al. 2012). Bears concentrate on pulses of fruit, small mammals or  
206 fish (Watts & Jonkel 1988), and even jackals may include a considerable proportion  
207 of fruits in their diet (Atkinson et al. 2002). During the wet season, lions favour zebras  
208 and wildebeest more than other prey species (Owen-Smith 2008), aided by  
209 concealing tall grass. In general, smaller prey species tend to be targeted by  
210 predators during the season of lesser vulnerability for herbivores.

211 Seasonality thus plays an important role in the feeding strategies of  
212 carnivores because it determines both the availability of carrion that can be exploited

213 as well as the vulnerability of prey species to being killed. This in turn has  
214 implications for intra-guild dynamics among carnivores, which is the topic of the next  
215 section.

216

## 217 **COMPETITION AND FACILITATION AMONGST CARNIVORES IN SEASONAL** 218 **ENVIRONMENTS**

219 Predators both facilitate scavengers by making the remains of their prey carcasses  
220 available, and compete with them by killing and consuming animals that would  
221 eventually have died and nourished the scavengers. Furthermore, carnivores  
222 towards both ends of the predator–scavenger continuum compete aggressively by  
223 killing other carnivores when opportunities present themselves (Palomares & Caro  
224 1999, Caro & Stoner 2003), and by stealing prey where possible through superiority  
225 in size or numbers (Cooper 1990, Honer et al. 2002). Creel et al. (2001) distinguish  
226 five forms of competition between carnivores, including active avoidance, avoidance  
227 leading to habitat shifts, dietary overlap, kleptoparasitism and killing. In more  
228 complex ecosystems, relationships become more complicated because by  
229 depressing the abundance of smaller carnivores, larger carnivores release  
230 populations of even smaller carnivores that were previously in competition with the  
231 middle sized carnivores (DeVault et al. 2011, Levi & Wilmers 2012). Nevertheless,  
232 facilitation remains the least well-documented relationship between carnivores  
233 (Steinmetz et al. 2008). What are the consequences for the coexistence of these  
234 species in seasonally variable environments?

235         In temperate ecosystems of North America, grey wolves have displaced  
236 coyotes as the primary predators on ungulates through their superior body and group  
237 size (Smith et al. 2003). Nevertheless, coyotes benefit from the remains of kills left by  
238 wolves, with this carrion particularly important in winters with low snow accumulation  
239 when few deer die of starvation (Wilmers & Getz 2004, 2005, Wilmers & Post 2006).  
240 North American wolves rarely scavenge (Metz et al. 2012). They leave little meat on

241 carcasses of the mainly young elk that they kill during summer, but more in winter  
242 when their prey selection shifts towards larger animals (Metz et al. 2012). During  
243 winter, coyotes benefit from these carcasses (Paquet 1992, Gese et al. 1996,  
244 Crabtree & Sheldon 1999, Wilmers & Getz 2004, 2005, Sala 2006). Thus top  
245 predators play a facilitative role in providing carcasses for other carnivores to  
246 scavenge outside of the season when carrion is abundant (Wilmers & Getz 2005, van  
247 Dijk et al. 2008). However, in Europe wolves commonly feed on carrion (e.g. Cuesta  
248 et al. 1991, Šmietana & Klimek 1993, Selva et al. 2003, Valdmann et al. 2005),  
249 depleting the food available to other scavengers. Nevertheless, in southern  
250 Scandinavia wolverines have benefitted from the recolonisation of by wolves through  
251 scavenging on kills of ungulates as large as moose (van Dijk et al. 2008). In  
252 Białowieża, wolves were the only vertebrate able to open deeply frozen European  
253 bison (*Bison bonasus*) carcasses, thus increasing scavenging opportunities for other  
254 species (Selva et al. 2003).

255         Competitive interactions among carnivores are strongly governed by relative  
256 body size. By limiting the abundance of coyotes through their size superiority, grey  
257 wolves allow foxes to thrive (Levi & Wilmers 2012). A comparable situation exists in  
258 Serengeti where locally high densities of lions and spotted hyenas are associated  
259 with a low density of cheetahs, but high densities of two jackal species (*C.*  
260 *mesomelas*, *C. aureus*; Durant et al. 2011). In the absence of wolves, coyotes kill  
261 more adult deer, benefitting from the higher proportion of aging adults and vulnerable  
262 offspring in these populations in these circumstances (Huegel & Rongstad 1985,  
263 Gese & Grothe 1995, Crabtree & Sheldon 1999, Prugh 2005). Under these  
264 conditions, coyotes outcompete and limit foxes that are likewise dependent mainly on  
265 small mammals during summer (Levi & Wilmers 2012).

266         In Africa, carrion is less readily available during wet season conditions when  
267 very few animals die of malnutrition. Furthermore, killing newly born calves provides  
268 less food than the carcasses of adult ungulates. At this time of the year, scavengers

269 depend more strongly on the carcass remains of animals killed by more capable  
270 predators (Henschel & Skinner 1990). Pursuit predators that undertake little or no  
271 scavenging, like cheetahs and wild dogs, are also disadvantaged during the wet  
272 season. Apart from juvenile prey, they must seek those few adults that can be  
273 overtaken because of injuries or advancing age (FitzGibbon & Fanshawe 1989). The  
274 paucity of this prey base may explain why both cheetahs and wild dogs cover vast  
275 home ranges at low density (Mills & Funston 2003). Both of these predators, the least  
276 powerful within the African large carnivore guild, also commonly lose animals they  
277 have killed to spotted hyenas and lions, and hence avoid regions where these larger  
278 species are abundant (Creel & Creel 1996, Durant 1998, Mills & Gorman 1997, Mills  
279 et al. 2004). However, large packs of wild dogs may hold one or two hyenas at bay  
280 while they rapidly devour meat from the kills they have made (Fanshawe &  
281 FitzGibbon 1993). Furthermore, cheetahs and wild dogs usually hunt during the day,  
282 thereby restricting kleptoparasitism by other predators that are mainly active  
283 nocturnally. Both species also incur direct mortality through being killed by lions and  
284 spotted hyenas, and have their distribution and abundance restricted as a result  
285 (Creel & Creel 1996, Durant 1998, Mills & Gorman 1997, Mills et al. 2004). Leopards  
286 also kill cheetahs sometimes (Palomares & Caro 1999), and commonly eat jackals  
287 and other small carnivores (Kruuk 1972, Schaller 1972).

288         The two African top carnivores (lions and spotted hyenas) interact intensely.  
289 Lions often kill hyenas, and hyenas can kill lions, especially as cubs (Palomares &  
290 Caro 1999). Lions and spotted hyenas generally overlap quite substantially in the  
291 ungulate species they hunt, but with regional variation (Hayward 2006, Owen-Smith  
292 2008, Owen-Smith & Mills 2008). Spotted hyenas hunt both zebra and wildebeest in  
293 Ngorongoro Crater where lions frequently scavenge on hyena kills (Kruuk 1972), but  
294 seldom do so in the Kruger Park (Owen-Smith & Mills 2008). Lions listen for the  
295 cackling sounds of hyenas during the night to locate carcasses of animals killed by  
296 hyenas (Houston 1974, Schaller 1972). While it is commonly believed that lions are

297 social to increase their hunting success, strength in numbers is also important in  
298 defending their kills against the packs formed by hyenas, and vice versa (Cooper  
299 1991, Honer et al. 2002). The relative density of lions versus hyenas appears to  
300 reflect the relative amount of hunting versus scavenging these competitors  
301 undertake, dependent on habitat conditions (Table 1). Spotted hyenas typically  
302 obtain one third or more of their food by scavenging in regions where their  
303 abundance is 1.5-2X that of lions, but in open grasslands they become mostly  
304 hunters and outnumber lions by a factor of four or more. Lions scavenge more where  
305 hyenas are more abundant. Scavenging from hyena kills helps lion prides survive in  
306 habitats deficient in the cover they need to stalk effectively, while hyenas persist in  
307 bushy areas where they cannot easily pursue prey over long distances by stealing  
308 carcasses from leopards (*P. pardus*; Pienaar 1969, Kruuk 1972, Bailey 1993).  
309 Another crucial adaptation of spotted hyenas is their capacity to subsist on the bones  
310 of carcasses left by lions. This ensures that these hyenas will always find some food,  
311 no matter how strong the predominance of lions at carcasses.

312           Distinctions in locomotory adaptations influence the extent to which large  
313 mammalian carnivores concentrate on found carcasses versus own kills as a food  
314 resource. Assisted by their loping gait, spotted hyenas can commute distances of 40-  
315 60 km between their dens and foraging areas, to get to places where prey species  
316 happen to be concentrated (Hofer & East 1993, 1995). To locate sufficient carcasses,  
317 the brown hyena, perhaps the best example of an obligate mammalian scavenger,  
318 wander on average 31 km and up to 54 km nightly, and may obtain over 90% of its  
319 food from animals found dead or the remains of predator kills (Mills 1990). They also  
320 commonly forage along shorelines where fish or seal carcasses wash up, earning the  
321 local name “strandwolf” (or “beach wolf”). In Serengeti, lions walked for on average  
322 only two hours per day, and no more than five hours even when actively hunting,  
323 thus covering at most 20 km (Schaller 1972). Wolverines are the prime scavengers in  
324 high northern latitudes, ranging widely to locate carcasses of animals that have died

325 in snow (Inman et al. 2012b). In summer they switch to becoming predators on  
326 newborn reindeer and caribou, as do foxes (Tveraa et al. 2003).

327 Mammalian carnivores compete for carcasses also with other vertebrate  
328 scavengers, invertebrates and decomposers. The Old World and New World vultures  
329 are the only obligate scavengers among vertebrates, exploiting their ability to soar  
330 widely, and thereby locate carcasses during times when few animals die, except  
331 through the agency of a predator (Ruxton & Houston 2004). The extremely efficient  
332 searching strategies of vultures, together with crucial physiological and  
333 immunological adaptations to counteract the potential lethal effects of toxins and  
334 pathogens (Houston & Cooper 1975), make them supremely adapted to exploit  
335 carrion (Houston 1979). Nevertheless, spotted hyenas can locate carcasses of  
336 animals that have died during the night before vultures become active, and hyenas  
337 and lions watch vultures during the day to find carcasses (Kruuk 1972, Schaller 1972,  
338 Houston 1979). Moreover, once they discover a carcass, large carnivores are able to  
339 displace vultures from the carcass, unless the vultures are present in very high  
340 numbers (Kruuk 1972). Mammalian carnivores that commonly scavenge seem  
341 adapted to deal with the toxins and pathogens that build up in carcasses with  
342 putrefaction, including the microparasites that might have caused the death of the  
343 animal (Cooper et al. 1999). While lions become infected with bovine tuberculosis  
344 from feeding on the buffalo they kill in the Kruger Park, and may suffer early death as  
345 a result, spotted hyenas feeding on these same carcasses seem unaffected, and  
346 appear immune to anthrax (Bengis et al. 2003).

347

#### 348 **CARRION SUBSIDY FROM MEGAHERBIVORE CARCASSES**

349 Megaherbivores like elephants (*Loxodonta africana*), hippopotami (*Hippopotamus*  
350 *amphibius*) and rhinoceroses (*Ceratotherium simum* and *Diceros bicornis*) are  
351 usually excluded from the prey base supporting predators (Sinclair et al. 2003,  
352 Owen-Smith & Mills 2008). Adults of these species are too large to be killed even by

353 lions, although immature animals remain vulnerable (Joubert 2006). Nevertheless,  
354 adults eventually die, and their carcasses become available for consumption by  
355 various carnivores. Animals of these species coming to the end of their potential  
356 lifespan would have been born 40-60 years ago, at a time when their populations  
357 were still recovering from the remnants left by human hunters earlier in the 20<sup>th</sup>  
358 century. This situation is now changing in many parks, and as the population  
359 structure stabilizes with lowered recruitment, death from old age will make an  
360 increasing contribution to mortality. How might this contribution to the carcasses  
361 available to carnivores affect the abundance of predators, and the balance between  
362 hunting and scavenging strategies?

363         Given a life expectancy of 60-70 years for elephants, and 40-50 years for  
364 hippos and rhinos, 2-3% of the adult segment would be expected to die annually  
365 once a stationary age distribution prevails, even if zero mortality occurred prior to the  
366 end of the lifespan. Megaherbivores typically constitute 40-70% of the herbivore  
367 biomass in intact African ecosystems (Owen-Smith 1988). Hence the food supply for  
368 carnivores scavenging opportunistically on these carcasses could be elevated by a  
369 third or more, resulting in higher carnivore densities and potentially more predation  
370 on smaller ungulates. An increase in predation risk for other herbivores by this  
371 proportion could tip their population trend from stable to decreasing.

372         However, megaherbivores succumbing to malnutrition die mainly during the  
373 late dry season and largely near surface water (Conybeare & Haynes 1984). This  
374 seasonal and spatial restriction limits the effective contribution of this food to  
375 supporting carnivore populations. Moreover, the time needed to consume such large  
376 carcasses makes them subject to greater putrefaction, restricting their utilization by  
377 predators less adapted to tolerate toxins and pathogens. Whatever the situation, the  
378 pulse of such easily available food could perhaps divert predation away from other  
379 prey species during this period.

380

## 381 **CONCLUSIONS**

382 In this review we have highlighted the seasonal variation that exists in the availability  
383 of food for carnivores, affecting competitive versus facilitative relationships along the  
384 continuum from predation to scavenging. We have outlined the more complex  
385 relationships that develop in the species-rich mammalian assemblages that persist in  
386 African savanna regions, compared with the more impoverished communities that  
387 remain in North America and Europe. Nevertheless, humans have had a substantial  
388 effect, even in Africa, quite recently by suppressing the contribution that  
389 megaherbivores formerly made to carcass production through decimating the  
390 populations of these beasts. Further effects continue today as humans eliminate the  
391 large predators that sometimes kill livestock and restrict the number of animals that  
392 die of old age.

393         The food supply for carnivores depends not only on the seasonal cycle of  
394 plentiful and sparse food for herbivores dependent on temperature and precipitation,  
395 but also on the local distribution, age structure and body condition of prey  
396 populations. From a simplistic perspective, carnivores need not be killers, because  
397 herbivores die eventually through reaching the end of the lifespan. One of the major  
398 problems, however, is that these deaths are likely to be seasonally pulsed. For  
399 carnivores to survive through the annual cycle, they must be able to secure sufficient  
400 food year-round. Hence, during wet season or summer conditions, carnivores turn to  
401 temporarily vulnerable segments of prey populations, including newly born young,  
402 heavily pregnant females, and males distracted or debilitated by breeding activities;  
403 and failing this, to small animals and fruits.

404         Ambush predators retain a greater chance of killing healthy prey  
405 opportunistically than cursorial predators, so that felids are more obligate hunters  
406 than canids, hyenids, ursids or mustelids. Northern temperate ecosystems currently  
407 lack a top ambush predator equivalent to African lions (Schaller 1972) or Asian tigers  
408 (Karanth & Sunquist 1995), following the extinction of the saber-tooth "cats"



409 (*Smilodon* spp) that were once the supreme ambush predators there. Grey wolves  
410 are the top predator by default, but by concentrating on smaller mammals during  
411 summer they leave little meat uneaten, forcing coyotes to hunt even smaller prey.  
412 While polar bears in the far north are primarily carnivorous (Derocher et al. 2002), the  
413 brown and grizzly bears syntopic with wolves are largely omnivorous. Wolverines fill  
414 the role of a scavenger that hunts opportunistically in the far north of both Eurasia  
415 and North America, but are restricted to regions where the snow cover persists well  
416 into spring (Inman et al. 2012a).

417 Relationships among African carnivores are complex, with both lions and  
418 spotted hyenas shifting in their role as primarily predators or scavengers depending  
419 on their relative numbers. Hyenas remain carnivores through being able to subsist on  
420 portions of carcasses inedible to lions, in particular bones, and also through being  
421 able to drive other carnivores from their kills. Hence despite being competitive, these  
422 carnivores are also interdependent. Although African wild dogs adopt a similar  
423 hunting technique to wolves, they remain much less abundant than wolves because  
424 lions and hyenas preemptively deplete the vulnerable segment from large ungulate  
425 populations, and compete directly for smaller ungulates. The paucity of scavenging  
426 by African wild dogs and cheetahs probably reflects their dismal prospects of gaining  
427 much thereby, although both of them do consume carcasses in captivity.

428 The comparison between Holarctic and African carnivore assemblages calls  
429 into question why in South America the scavenger niche is filled entirely by birds  
430 (Keast 1969). Mammalian scavengers were represented by borhyaenids into the  
431 Pliocene (Marshall et al. 1982), but the placental carnivores that replaced them had  
432 no equivalent. The numerous equids and gomphotheres that existed in South  
433 America until the terminal Pleistocene (Webb 1977) would have provided an  
434 abundance of carcasses, albeit only seasonally in the absence of a top predator.  
435 Extant jaguar (*P. onca*) and puma subsist primarily on deer and peccaries (Aranda &  
436 Sánchez-Cordero 1996). Jaguars occasionally scavenge on cattle carcasses (López-

437 González & Piña 2002), in the absence of competition from any more obligate  
438 mammalian scavenger.

439         The limiting time for carnivores is when their herbivore prey are well-  
440 nourished and hence robust, which is during the summer or wet season months. The  
441 success of scavengers may then be crucially dependent on the presence of  
442 predators able to kill large ungulates and thereby provide large carcasses even at  
443 this time of the year; a situation that now persists solely in Africa and tropical Asia.  
444 The indirect cascading effects in food webs initiated by carrion shortages can be  
445 magnified by human hunting. On the one hand, intensive game hunting restricts the  
446 proportion of wild ungulate populations attaining terminal senescence and thus the  
447 carcasses produced by causes other than predation. On the other hand, hunting can  
448 lead to a carrion surfeit in areas where disposal of hunting leftovers from the field is a  
449 common practice (Wilmers et al. 2003). In Africa, subsidies from megaherbivore  
450 carcasses may disrupt pre-existing patterns of hunting versus scavenging, with  
451 ramifying consequences for prey populations.

452         Human impacts can have further, indirect implications for mammalian  
453 carnivores. Northern temperate ecosystems have been shown to be highly  
454 vulnerable to global climatic change. Global warming has been associated with a  
455 shorter period with deep snow during winter in Yellowstone National Park, reducing  
456 the number of ungulates dying from starvation, and hence the supply of carcasses to  
457 carrion-reliant species during this period (Wilmers & Getz 2005). However, the  
458 carcasses contributed through predation by wolves, together with the opening of  
459 intact carcasses of large ungulates by these top carnivores, counteract the food  
460 bottleneck to some extent. Here, the protection of top carnivores, widely threatened  
461 worldwide (e.g. Gittleman et al. 2001), is essential for maintaining the entire  
462 ecosystem. Global warming consequences on ungulate mortality patterns in African  
463 savannas could be very different. There, an expansion of the dry period might

464 increase the number of herbivores succumbing to malnutrition and diseases, thus  
465 producing more carcasses to be consumed by opportunistic scavengers.

466 Finally, long-distance herbivore migrations have been largely constrained in  
467 Africa over the last two centuries due to human pressure and to the fencing of  
468 protected reserves. This could dramatically affect the carrion subsidies available in  
469 some areas, thus diminishing scavenging opportunities for carnivores and increasing  
470 predation pressure on prey populations. Ultimately protected areas may become too  
471 small to conserve viable populations of the larger carnivores, with consequences  
472 ramifying through the food web.

473 Overall, we must recognise that relationships among carnivores based on  
474 hunting versus scavenging strategies are flexible and subject to changes in response  
475 to prevailing circumstances. This functional complexity must be taken into account  
476 when assessing the consequences of global change for ecosystem function.

477

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481

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