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Citation: Pereira, L., Owen-Smith, N. & Moleon, M. (2013). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal review*, 44(1), pp. 44-55. doi: 10.1111/mam.12005

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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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40 Word count: 8636

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42 Please cite as: Pereira, L.M., Owen-Smith, N. and Moleon, M. (2013) Facultative
43 predation and scavenging by mammalian carnivores: seasonal, regional
44 and intra-guild comparisons. *Mammal Review*, DOI: 10.1111/mam.12005.

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 20th
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

478 **ACKNOWLEDGEMENTS**

479 The last author was supported by a postdoctoral grant from the Spanish Ministry of
480 Education (Plan Nacional de I+D+i 2008-2011).

481

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