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

Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons

ABSTRACT

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

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

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

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

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

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

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

Running head: Predation versus scavenging in carnivores

Word count: 8636

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

INTRODUCTION

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

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

In this article we propose as a null foundation that all carnivores have to do to feed is wait until animals eventually succumb to the debilitating effects of advancing age. In practice this is untenable, recognizing the intense competition among other scavengers and decomposers for the rich food constituted by animal body tissues (Wilson & Wolkovich 2011). Hence, helping animals die a little sooner can gain prior access to the meat. However, the energy costs associated with hunting are high, especially for large mammals; for instance, transport costs for the largest carnivores (lions –*Panthera leo*– and polar bears –*Ursus maritimus*–) are 2-3 times higher than expected for their size (Carbone et al. 2007). The challenge that carnivores face is how to secure a regular supply of food when the susceptibility of animals to die or be killed varies seasonally and spatially. As a result, most large mammalian carnivores shift facultatively between hunting and scavenging depending on seasonal and regional variation in the susceptibility of their prey to mortality.

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

Recent reviews addressing overlaps between scavenging and hunting have been orientated towards northern ecosystems, which retain somewhat impoverished remnants of their former carnivore complement (Jędrzejewski et al. 1993, DeVault et al. 2003, Cortés-Avizanda et al. 2009). Those addressing African ecosystems with largely intact carnivore assemblages have emphasised predation and its consequences, rather than the scavenging that also takes place (Sinclair et al. 2003, Hayward 2006). We aim to balance this oversight by considering how large mammalian carnivores cope with seasonal variation in food availability through flexibility in their feeding strategies from strict predation to mainly scavenging. In particular, we address the following questions: (1) How do carnivores cope with the seasonal period when prey are least vulnerable to mortality?; (2) How does facultative scavenging or predation affect competitive or facilitative relationships among carnivores?; (3) How do these patterns differ between depauperate northern communities and intact African ones?; (4) How do human activities alter trophic interactions and fluxes through predation versus scavenging?

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

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

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

Migratory movements also affect the patterns of both ungulate mortality and vulnerability to predation. In Serengeti, deaths not mediated by predation are amplified by the huge local concentrations of migrants, saturating the capacity of resident predators to exploit them. Spotted hyenas (*Crocuta crocuta*) commute long distances to reach places where these ungulates are concentrated (Hofer & East 1993). Hence, migratory wildebeest, zebra (*Equus quagga*) and Thompson's gazelle (*Eudorcas thomsonii*) form the majority of spotted hyena's diet in the Serengeti plains despite only being available there for 26% of the year (Hofer & East 1993). When these migratory ungulates reach the Kenia's Masai Mara region during the dry season, they greatly increase the supply of carrion there. The desiccated carcasses help support carnivores after the migrants have left (Cooper et al. 1999). In Africa, buffalo become most vulnerable to predation on adults when at their weakest during the transition period around the start of the rains (Owen-Smith 2008).

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

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

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

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

Seasonality thus plays an important role in the feeding strategies of carnivores because it determines both the availability of carrion that can be exploited as well as the vulnerability of prey species to being killed. This in turn has implications for intra-guild dynamics among carnivores, which is the topic of the next section.

COMPETITION AND FACILITATION AMONGST CARNIVORES IN SEASONAL ENVIRONMENTS

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

In temperate ecosystems of North America, grey wolves have displaced coyotes as the primary predators on ungulates through their superior body and group size (Smith et al. 2003). Nevertheless, coyotes benefit from the remains of kills left by wolves, with this carrion particularly important in winters with low snow accumulation when few deer die of starvation (Wilmers & Getz 2004, 2005, Wilmers & Post 2006). North American wolves rarely scavenge (Metz et al. 2012). They leave little meat on carcasses of the mainly young elk that they kill during summer, but more in winter when their prey selection shifts towards larger animals (Metz et al. 2012). During winter, coyotes benefit from these carcasses (Paquet 1992, Gese et al. 1996, Crabtree & Sheldon 1999, Wilmers & Getz 2004, 2005, Sala 2006). Thus top predators play a facilitative role in providing carcasses for other carnivores to scavenge outside of the season when carrion is abundant (Wilmers & Getz 2005, van Dijk et al. 2008). However, in Europe wolves commonly feed on carrion (e.g. Cuesta et al. 1991, Śmietana & Klimek 1993, Selva et al. 2003, Valdmann et al. 2005), depleting the food available to other scavengers. Nevertheless, in southern Scandinavia wolverines have benefitted from the recolonisation of by wolves through scavenging on kills of ungulates as large as moose (van Dijk et al. 2008). In Białowieża, wolves were the only vertebrate able to open deeply frozen European bison (*Bison bonasus*) carcasses, thus increasing scavenging opportunities for other species (Selva et al. 2003).

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

In Africa, carrion is less readily available during wet season conditions when very few animals die of malnutrition. Furthermore, killing newly born calves provides less food than the carcasses of adult ungulates. At this time of the year, scavengers depend more strongly on the carcass remains of animals killed by more capable predators (Henschel & Skinner 1990). Pursuit predators that undertake little or no scavenging, like cheetahs and wild dogs, are also disadvantaged during the wet season. Apart from juvenile prey, they must seek those few adults that can be overtaken because of injuries or advancing age (FitzGibbon & Fanshawe 1989). The paucity of this prey base may explain why both cheetahs and wild dogs cover vast home ranges at low density (Mills & Funston 2003). Both of these predators, the least powerful within the African large carnivore guild, also commonly lose animals they have killed to spotted hyenas and lions, and hence avoid regions where these larger species are abundant (Creel & Creel 1996, Durant 1998, Mills & Gorman 1997, Mills et al. 2004). However, large packs of wild dogs may hold one or two hyenas at bay while they rapidly devour meat from the kills they have made (Fanshawe & FitzGibbon 1993). Furthermore, cheetahs and wild dogs usually hunt during the day, thereby restricting kleptoparasitism by other predators that are mainly active nocturnally. Both species also incur direct mortality through being killed by lions and spotted hyenas, and have their distribution and abundance restricted as a result (Creel & Creel 1996, Durant 1998, Mills & Gorman 1997, Mills et al. 2004). Leopards also kill cheetahs sometimes (Palomares & Caro 1999), and commonly eat jackals and other small carnivores (Kruuk 1972, Schaller 1972).

The two African top carnivores (lions and spotted hyenas) interact intensely. Lions often kill hyenas, and hyenas can kill lions, especially as cubs (Palomares & Caro 1999). Lions and spotted hyenas generally overlap quite substantially in the ungulate species they hunt, but with regional variation (Hayward 2006, Owen-Smith 2008, Owen-Smith & Mills 2008). Spotted hyenas hunt both zebra and wildebeest in Ngorongoro Crater where lions frequently scavenge on hyena kills (Kruuk 1972), but seldom do so in the Kruger Park (Owen-Smith & Mills 2008). Lions listen for the cackling sounds of hyenas during the night to locate carcasses of animals killed by hyenas (Houston 1974, Schaller 1972). While it is commonly believed that lions are social to increase their hunting success, strength in numbers is also important in defending their kills against the packs formed by hyenas, and vice versa (Cooper 1991, Honer et al. 2002). The relative density of lions versus hyenas appears to reflect the relative amount of hunting versus scavenging these competitors undertake, dependent on habitat conditions (Table 1). Spotted hyenas typically obtain one third or more of their food by scavenging in regions where their abundance is 1.5-2X that of lions, but in open grasslands they become mostly hunters and outnumber lions by a factor of four or more. Lions scavenge more where hyenas are more abundant. Scavenging from hyena kills helps lion prides survive in habitats deficient in the cover they need to stalk effectively, while hyenas persist in bushy areas where they cannot easily pursue prey over long distances by stealing carcasses from leopards (*P. pardus*; Pienaar 1969, Kruuk 1972, Bailey 1993). Another crucial adaptation of spotted hyenas is their capacity to subsist on the bones of carcasses left by lions. This ensures that these hyenas will always find some food, no matter how strong the predominance of lions at carcasses.

Distinctions in locomotory adaptations influence the extent to which large mammalian carnivores concentrate on found carcasses versus own kills as a food resource. Assisted by their loping gait, spotted hyenas can commute distances of 40-60 km between their dens and foraging areas, to get to places where prey species happen to be concentrated (Hofer & East 1993, 1995). To locate sufficient carcasses, the brown hyena, perhaps the best example of an obligate mammalian scavenger, wander on average 31 km and up to 54 km nightly, and may obtain over 90% of its food from animals found dead or the remains of predator kills (Mills 1990). They also commonly forage along shorelines where fish or seal carcasses wash up, earning the local name “strandwolf” (or “beach wolf”). In Serengeti, lions walked for on average only two hours per day, and no more than five hours even when actively hunting, thus covering at most 20 km (Schaller 1972). Wolverines are the prime scavengers in high northern latitudes, ranging widely to locate carcasses of animals that have died in snow (Inman et al. 2012b). In summer they switch to becoming predators on newborn reindeer and caribou, as do foxes (Tveraa et al. 2003).

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

CARRION SUBSIDY FROM MEGAHERBIVORE CARCASSES

Megaherbivores like elephants (*Loxodonta africana*), hippopotami (*Hippopotamus amphibius*) and rhinoceroses (*Ceratotherium simum* and *Diceros bicornis*) are usually excluded from the prey base supporting predators (Sinclair et al. 2003, Owen-Smith & Mills 2008). Adults of these species are too large to be killed even by lions, although immature animals remain vulnerable (Joubert 2006). Nevertheless, adults eventually die, and their carcasses become available for consumption by various carnivores. Animals of these species coming to the end of their potential lifespan would have been born 40-60 years ago, at a time when their populations were still recovering from the remnants left by human hunters earlier in the 20th century. This situation is now changing in many parks, and as the population structure stabilizes with lowered recruitment, death from old age will make an increasing contribution to mortality. How might this contribution to the carcasses available to carnivores affect the abundance of predators, and the balance between hunting and scavenging strategies?

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

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

CONCLUSIONS

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

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

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

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

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

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

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

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

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

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

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

ACKNOWLEDGEMENTS

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

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